

## PLENARY ADDRESSES

### THE PAST OF SPONGES — SPONGES OF THE PAST

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*Astra Pharmaceuticals (Australia) Plenary Address*



Debrenne, F. 1999 06 30: The past of sponges, sponges of the past. *Memoirs of the Queensland Museum* 44: 9-21. Brisbane. ISSN 0079-8835.

Fossil sponges lack many of the features seen in living sponges, with the consequence that their traditional taxonomy was nearly completely reliant on preserved skeletal architectural characteristics, producing a fossil sponge classification that had diverged considerably from that of living sponges. Subsequent discoveries of 'living fossil' sponges with hypercalcified basal skeletons, representing some of the groups thought to be long extinct, provided a revolutionary basis to solve some of the palaeontological enigmas and to comprehensively revise the groups themselves. Ancient groups sphinctozoans, stromatoporoids and chaetitids, with species in Recent seas, are now recognised as grades of construction rather than clades of taxa. The existence of these 'living fossil' sponges provided an unique opportunity to compare tissues, spicules and microstructures of the basal skeleton with well preserved fossil material; to understand the influences of biomineralisation and diagenetic alterations affecting mineral composition and microstructures in fossil sponges and to infer the systematic position of Paleozoic to Recent sponges with a calcified skeleton. Similar conclusions were reached for the archaocyaths, with no living representative yet recorded, but with structural features consistent with the Phylum Porifera. More recent discoveries of ancient sponge tissues and larvae from Precambrian phosphorites provide even more valuable data on the early history and development of Demospongiae and Calcarea, extending the age of the latter group considerably. □ *Porifera, palaeontology, hypercalcified basal skeleton, sphinctozoans, stromatoporoids, chaetitids, archaocyaths, taxonomie overview.*

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We know from the old literature that living sponges have been known since Ancient Times, being familiar household items in ancient Greece and Rome. During the Middle Ages burned sponges were reputed to have therapeutic value in the treatment of various diseases, perhaps anticipating their present pharmaceutical use! Conversely, discoveries of fossil sponge-like 'objects' occurred much latter. These were first figured and described as 'mushrooms' at the end of the 16th century in the Moscardo collection, according to Zittel (1883). Other scattered examples of sponge-like objects were published later, but these authors did not know whether these forms were plants or zoophytes (Fig.1). The first valuable observations were made in the second half of the 18th century by Guettard (1768-1783) and several other authors at the beginning of the 19th century. These authors compared their fossils to Alcyonaria or horny corals, but not to recent sponges. Goldfuss (1826) first suggested these fossil forms may be related to living horny sponges, which subsequently mineralised into silica or calcium carbonate, and

they attributed known fossil forms to Recent sponge genera.

With the ensuing discovery of Hexactinellida (or Hyalosponges) from deepwater dredgings, the exact position of some fossils was established (auguring the impact of the future discovery of 'living fossil' hypercalcified sponges or sclerosponges).

D'Orbigny (1849-1850) proposed an initial classification of fossil sponges based on external characters. He considered that these fossil sponges, the *Petrospongia*, a nearly extinct group, had a mainly calcareous 'stony' skeleton, contrary to previous interpretations whereby the horny skeleton became secondarily mineralised. De Fromentel's (1889) classification took into account the interlocking pattern of fibers, the shape of spicules and characteristics of the canal system, but it still kept separate the fossil group *Spongitaria*, amorphozoans with 'testacean' skeleton, and the extant group *Spongia*, amorphozoans with horny skeleton.

The existence of siliceous sponges in the fossil record was confirmed by the discovery of spicules in Jurassic and Cretaceous rocks. The

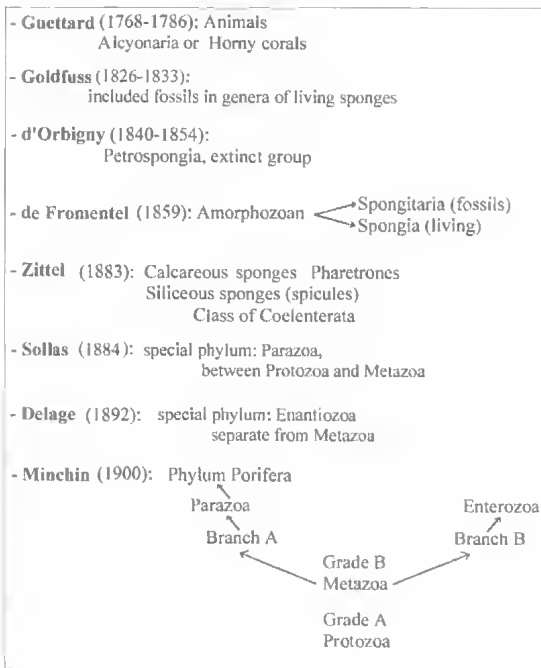


FIG. 1. Plants or zoophytes?

existence of calcareous and siliceous fossil sponges was recognised in the 1870s, but at that time specialists were unable to distinguish the two groups because of secondary replacement of calcium by silica, and vice versa. Zittel (1885), pioneering microscopic studies on sponge structures, described the anastomosing fibers in the skeleton of calcareous sponges (pharetrones), clearly differentiating them from siliceous spicules of other sponges. He concluded from studies on microstructures of fossil and recent forms that they both belonged to the same 'Class' among Coelenterata. By comparison, Sollas (1884) included them in the Phylum Porifera, in a group Parazoa intermediate between the Protozoa and Metazoa, whereas Delage (1892) created a special group, the Enantiozoa, separated from Metazoa.

By the end of 19th century the first act of the 'Fossil Sponge Story' had closed. Minchin (1900) established the essential features: sponges were animals and the most primitive phylum of the Metazoa. The main lines of classification were recognised: those with calcareous spicules or skeletons were included in the class Calcarea; those with siliceous spicules bearing 3 axes arranged to form hexactines were included in the class Hexactinellida; and those with a spongin skeleton, or a spongin skeleton and siliceous

spicules, or only with siliceous spicules lacking 3 axes were included in the class Demospongiae.

The description of new genera in time and space raised the problem of their systematic position within families and orders. During Zittel's (1883) time there were few taxa or only the non-identifiable remains of sponges available on which to base a classification. The predominance of Cainozoic and Mesozoic forms reflected the bias of stratigraphical investigations more so than an evolutionary trend. Rapidly, however, the number of genera increased as monographs were published throughout the world. De Laubenfels (1955) noted that more than 1,000 genera have been established for fossil sponges.

Since that time techniques in preparation and methods of investigations had improved progressively such that the number of new taxa, and the number of 'significant characters' upon which to differentiate taxa, had both significantly increased. Similarly, and inevitably, there has been disagreement amongst authors concerning the relative importance of certain characters over others, and different interpretations of the development of new structures and new forms from the existing ancestral forms. As a consequence, the systematics of living and fossil sponges have diverged substantially, developed independently, and are now based on largely different criteria.

Living sponges have a relatively large pool of morphological and other biological characters that are potentially useful for classification. Their skeletons are made of various materials ranging from organic spongin to mineralised spicules or aspicular elements. In addition to skeletal characteristics, they are also classified on the basis of their biological activity, biochemistry, methods of reproduction, and several other useful characters related to their soft parts and cellular constituency. The fossilisation potential of sponges is also very variable. With some rare exceptions, sponges with isolated spicules are fossilised only as scattered skeletal elements, accounting for the numerous gaps in the fossil record. After death spicules are usually dispersed amongst the sediments and sometimes dissolved in the seawater, but in some cases rapid sedimentation has buried or winnowed sponges in favourable environments (such as in back reef lagoons and volcanic products), with a few fossils much better preserved. Moreover, the diagnostic value of isolated spicules may be poor given that many of the major spicule types are

present in several orders, even in different classes. The best fossils concern species with a skeleton built by fused spicules (such as 'lithistid' construction), and most sponges with solid skeletons (such as compressed skeletons or hypercalcified sponges) also provide reasonable fossil material. Bodily preserved sponges are often diagenetised, the spicules in place also often dissolved or recrystallised.

By comparison, fossil sponges lack many of the features useful for taxonomy of living sponges, relying largely on features of preserved skeletal architecture. Fortunately, some fossil forms are known through a miracle of preservation (lagerstätten), and comparisons between these fossil species and so-called 'living fossil' sponges from Recent seas provide opportunities to reinterpret the palaeo-environment. The importance and meaning of calcification in sponges became evident following the discovery of the Jamaican 'coralline sponges'. These hypercalcified sclerosponges have a compound basal skeleton of aragonite together with organic fibers and free siliceous spicules (Hartman & Goreau, 1970), demonstrating that there were several permutations to the concept of calcitic skeletons, not limited to possession of only calcified spicules or to possession of a solid calcareous skeletons devoid of spicules. The class Sclerospongiae was erected for these sponges, with an indication they may be the living representatives of some Mesozoic and Paleozoic cnidarian-like fossils.

It was a conceptual revolution: the systematic position of some enigmatic groups long thought to be extinct, such as the reef-building archaeocyaths, stromatoporoids, sphinctozoans and chaetetids, each previously attributed to independent phyla or to Cnidaria in the case of the latter, were considered in a completely new light. As an ancient sponge fauna has living remnants in Recent seas, it is possible to compare the fissure and the spicules of these 'living fossils' with those of other modern forms, and to infer the systematic position of Paleozoic to Recent forms with a hypercalcified skeletons. I will discuss each of these groups separately.

**ARCHAEOCYATHS.** One of the main problems in assigning archaeocyaths to the Porifera is the absence of spicules in the hypercalcified skeleton, but Jean Vacelet's (1964) work on *Petrobiona massilliana* provided a basis for direct comparison between Recent and fossil sponges with hypercalcified skeletons but lacking free spicules. Nevertheless, at that time we were still

uncertain of their affinities, so we left the archaeocyaths in their own, extinct phylum, close to, but different from Porifera. At the London Symposium in 1967 Ziegler & Rietschel (1970) stated that none of the features shown by archaeocyaths really conflict with the possibility they may be sponges. In contrast, in the same volume Zhuravleva (1970) created a new sub-phylum, the Archaeozoa, of equal rank with Parazoa and Enterozoa, more similar to Protozoa than to Porifera, and included in it the Sphinctozoa and other enigmatic extinct multicellular animals. This latter group, called the 'Archaeata', included archaeocyaths, sphinctozoans, aphrosalpingidids and receptaculitids, and resided somewhere between animals and plants. Finally, this kingdom was subdivided into Aphrosalpingata and Inferibionta (Fig. 2), which combined archaeocyaths and sphinctozoans. This view was not so far from the general opinion of the time, except the suggestion that Inferibionta might have originated from the Eukaryotes, independently from all other kingdoms.

At the Washington 'Fossil Cnidarian Symposium' in 1980, in light of recent discoveries, Jean Vacelet and I re-examined the question of archaeocyath affinities (Debrenne & Vacelet, 1984). Much progress had been made on archaeocyath studies between 1967 and 1980. Studies on their functional morphology (indicating that they were filter feeders), ontogenetic stages, microstructural analysis of primary and secondary skeletons (supporting the concept of their monophyly, despite the great diversity of morphologies), allowed more precise comparisons to be made between archaeocyaths and sponges. Moreover, discoveries of Antarctic archaeocyaths and of Australian sphinctozoans in the Upper Cambrian narrowed the stratigraphic gap between the two groups. Detailed comparisons with the Recent species *Vaceletia crypta* (Vacelet, 1977) led us to conclude that secretion of both the primary and secondary skeleton proceeds by rapid mineralisation, and that none of the structural features of an archaeocyath were inconsistent with a sponge model. Further studies by A. Yu. Zhuravlev (1989) and P. Kruse (1990) reinforced the hypothesis that archaeocyaths are poriferans. The pattern of immune reactions, the type of asexual reproduction and the presence of crypt cells suggest that they are closer to demosponges than to other classes of sponges (Debrenne & Zhuravlev, 1994).

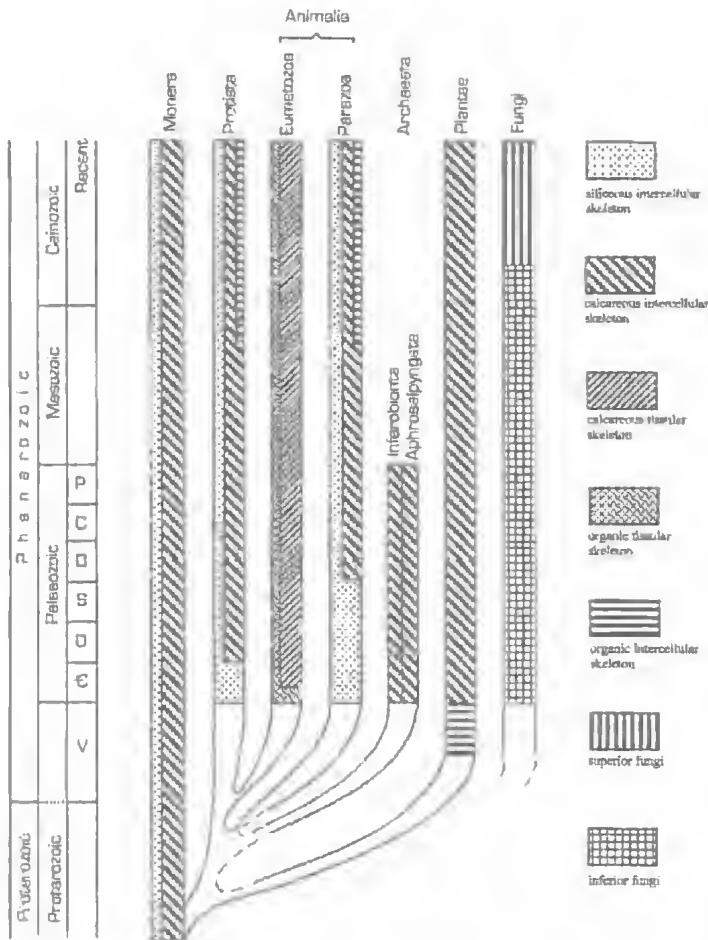


FIG. 2. Archaeatha in the organic world, after I. I. Zhuravleva & E. J. Miagkova, 1979, modified.

**SPHINCTOZOANS** *Vaeclitia crypta*, and its possibly intraspecific colonial form (Vaeclit et al., 1992), were discovered in cryptic habitats. Both presented a series of successive hemispherical chambers, reminiscent of the Sphinctozoa, and at that time they were included as one of the two orders of Pharetronida. For palaeontologists, Pharetronida (simple Inozoa and segmented Sphinctozoa) belong to the Calcarea. However, the histology, cytology and sexual reproduction of *Vaeclitia* are similar to those of the Ceractinomorpha in the class Demospongiae. Consequently, the systematic position of sphinctozooan sponges is questionable and must be re-evaluated.

The lack of spicules in *Vaeclitia* could explain the absence of spicules in some fossil sphinctozooan forms. Vaeclit (1979, 1985), Pickett (1982)

and Pickett & Jell (1983) placed most of the Sphinctozoa (including those lacking spicules) into Demospongiae, whereas segmented sponges with calcite spicules were retained in Calcispongia (Calcarea). For H. & G. Termier (Termier & Termier, 1975, 1977) all Pharetronida (Sphinctozoa and Inozoa) belonged to a primitive group Ischyrospongia, originating from stromatoporoid-chaetetid stock, and with archaeocyaths as a close group of ancestors stemming from the Cambrian. This proposal has been heavily criticised by many workers due to the highly polyphyletic nature of this collection of fossils.

It is now admitted that the chambered calcareous skeleton seen in sphinctozooans is a convergent feature, having arisen many times within the classes Demospongiae and Calcarea. Evidence indicated that sponges were able to produce these sorts of skeleton with relatively ease (Vaeclit, 1985; Wood, 1987; 1990), and that the concept of Sphinctozoa was artificial, a grade of construction, and not a systematic clade. This grade of organisation can also be found in archaeocyaths (Debrénne & Wood, 1990).

Sphinctozoa has been included in Calcarea since Steinman (1882); the problem was only to move them within the classes of Porifera; but it was not easy to admit for some time that most sphinctozooans were Demospongiae, as indicated by more reliable taxonomic criteria concerning the soft tissue and spicule form.

**STROMATOPOROIDS AND CHAETETIDS.** It was even more difficult to assess the affinities of these groups, whose systematic positions have long been disputed. Palaeontologists had generally accepted that Stromatoporoidea and Chaetetida had affinities to Hydrozoa. This position required reassessment, however, with the discovery of *Acanthochaetetes* by Hartman & Goreau (1975), with this new genus assigned to a Mesozoic chaetetid. As a consequence,

Paleozoic and Mesozoic chaetetids were considered to have Poriferan affinities due to their similarity with these 'living fossils'. Like sphinctozoans, the stromatoporoids and chaetetids were polyphyletic and represented grades of organisation rather than systematic clades. These grades are also known in the archaeocyaths (Table 1).

'LIVING FOSSILS'. New discoveries in the Mesozoic and the Paleozoic fossil record since the 1970s, by researchers such as Cuif, Dieci and their teams, Wendt, Kazmierczak, H. & G. Termier and others, dramatically increased the number of forms assigned to 'sclerosponges'. These discoveries provided a larger diversity of taxa to further compare with the few known Recent species, but they also led to many different hypotheses on their affinities and systematics, sometimes leading to further confusion.

The discovery of 'living fossils' certainly settled some enigmas, but it also led to the recognition that the existing taxonomy and phylogenetic grouping within Porifera required substantial revision. Vacelet (1985) showed that living sclerosponges were a collection of assorted demosponges, which can be distributed easily within pre-existing orders and families, and that the class Sclerospongiae was polyphyletic and unnecessary. He also found that many hypercalcified forms had closely related non-calcified equivalents. As a result, he invited palaeontologists to apply and test his phylogenetic proposals to the fossil record.

Because they lack many of the characteristics seen in living species, fossil forms are difficult to compare directly to living taxa, and thus it is difficult to test all of Vacelet's (1985) criteria. 1) The presence of siliceous spicules in hypercalcified skeletons is still a matter of debate, as the structures observed in fossil forms are moulds which could be interpreted equally as well as either cavities or calcareous modified spicules (argument used by Rigby & Webby, 1985 to maintain the Sphinctozoa in the Calcarea). 2) Minute details of macroscleres, such as small

TABLE 1. List of the various proposal of affinity for Stromatoporoids, after R.A. Wood, 1987, modified.

Anthozoa (not including tabulate corals)	Porifera	Bryozoa
Goldfuss 1826 De Blainville 1833 Lonsdale 1840 Römer 1843 Von Keyserling 1843 Hall 1847 McCoy 1851 Billings 1862 Lindström 1880 Mori 1976,1984	Steininger 1834 D'Orbigny 1850 Eichwald 1860 Von Rosen 1869 Salter 1873 Nicholson 1873 Sollas 1877 Nicholson & Murie 1878 Solomko 1886 Kirkpatrick 1912 (Aug) Heinrich 1912 Twitchell 1929 Hartman & Goreau 1970,1972 Stearns 1972,1975 Wendt 1975,1979,1984 Hartman 1979 Stock 1984 Wood 1986	Römer 1851 Sandberger & Sandberger 1850
Hydrozoa	Cyanobacteria	Tabulate corals
Lindström 1873 Carter 1877,1880 Zittel 1877 Steinmann 1878 Champemowne 1879 Bargatsky 1880 Nicholson 1886 Yabe & Sugiyama 1920, 1935 Delhomme 1920 Steiner 1935 Lecompte 1952,1956 Hudson 1955,1960 Flügel 1958 Turnšek 1960,1974 Kazmierczak 1971 Turnšek & Masse 1974	Kazmierczak 1976, 1983	Römer 1856 Nestor 1981
Foraminifera	'Vegetable'	Cephalopoda
Dawson 1875, 1879 Lindström 1870 Kirkpatrick 1912 (Sept) Hickson 1934 Parks 1935	Billings 1857	Hyatt 1865

ornamentations important for differentiating living taxa, are rarely observed in fossils. 3) Similarly, the large diversity of spicules (including microscleres) so common in living species is generally unknown in the fossil record. 4) The possession of a hypercalcified skeleton remains the principal source of information for palaeontologists to assess relatedness, whereas gross morphological characters cannot be used, given the high probability of architectural convergences. 5) As a consequence of these problems, palaeontologists have devised other ways to investigate affinities, such as growth pattern, type of skeletal microstructures, mineralogy, biochemistry of intraskeletal organic material (Gautret, 1989). 6) The systematic importance of the microstructure of hypercalcified skeletons has also been disputed. Wendt (1979)

Grade of organisation	Groups of organisms	Growth Pattern			
Systematic groups	Stromatoporoidea PZ				
	Stromatoporoidea MZ				
	Chaetetida				
	Sphinctozoa				
	Sclerospongiae				
	Archaeocyatha				
	Ceractinomorpha				
	Tetractinomorpha				
	Homoscleromorpha				
	Calcaronea		?		
	Calcinea		?	?	
	Hexactinellida				

FIG. 3. Grades of organisation in the different systematics groups, after F. Debrenne & A. Zhuravlev, 1992, modified.

proposed that diagenetic modifications to primary skeletal structures might be useful. He suggested through carefully study of the size, shape and arrangement of microstructural units, and the composition of intraskeletal organic compounds, that these characters appear to be biologically controlled. 7) Another problem concerns inconsistencies in the terminology used by different authors to describe hypercalcified sponge skeletons, whereby the same term can be used to describe different skeletal types. For example, spherulitic structures in *Petrobiona* and *Astrasclera* are clearly distinct and may define these taxa (Gautret, 1986), yet global statements such as 'non-taxonomic value of calcareous microstructures' have been proposed since the 1970s.

Thus, the challenge to palaeontologists proposed by Jean Vacelet (1985) seemed impossible

to address: we were unable to use structural morphology and microstructural features were not really recognised.

**MICROSTRUCTURAL FEATURES.** Two questions were asked by Jean-Pierre Cuif and his team in Paris-Sud-Orsay University: 1) Is it possible to obtain significant data on microstructure of the various calcified tissues, at the same time avoiding confusion between them, even in fossils suffering some diagenetic alterations? 2) What is the probability that identical modes of secretion of skeletal structures exist in distantly related, or unrelated, taxa?

The microstructural elements on fossils are 'biologically finished' and more-or-less diagenetically transformed structures. Pascale Gautret had already been studying skeletal structures of Recent hypercalcified sponges since 1986, examining in particular the living tissues responsible for their secretion, and not restricting research to the typology of fossils microstructures as most of those before her. She re-examined the different microstructures known to occur during ontogenetic development of skeletal formation, as well as the growth pattern of microstructural elements. She used the same methodology for living and fossil taxa, and was able to redefine the concept of 'microstructure' and to resolve differences in microstructures at a higher resolution. Validation of microstructural criteria was confirmed through biochemical analysis and ultrastructural analysis of organo-mineral components, through selective separation of mineral and the organic intraskeletal material using different reagents and appropriated observation techniques (Gautret & Marin, 1990; Marin & Gautret, 1994).

At about the same time as Gautret's team was working on this problem, Cuif's group completed an ultrastructural analysis of microcrystals using chromatography (evolution curves, molecular weights, comparison of the soluble matrix) and X-ray mapping (used for in situ characterisation of fossil skeletal material based on the premise that there is a reduction of the mean molecular weight during their diagenetic evolution). Cuif's group also examined amino acid and monosaccharide composition of the soluble organic matrix of both fossils and Recent sponges. They found that each type of biomineralisation process involved specific organic material, confirming that particular combinations of organic components may be characteristic of particular skeletal types.

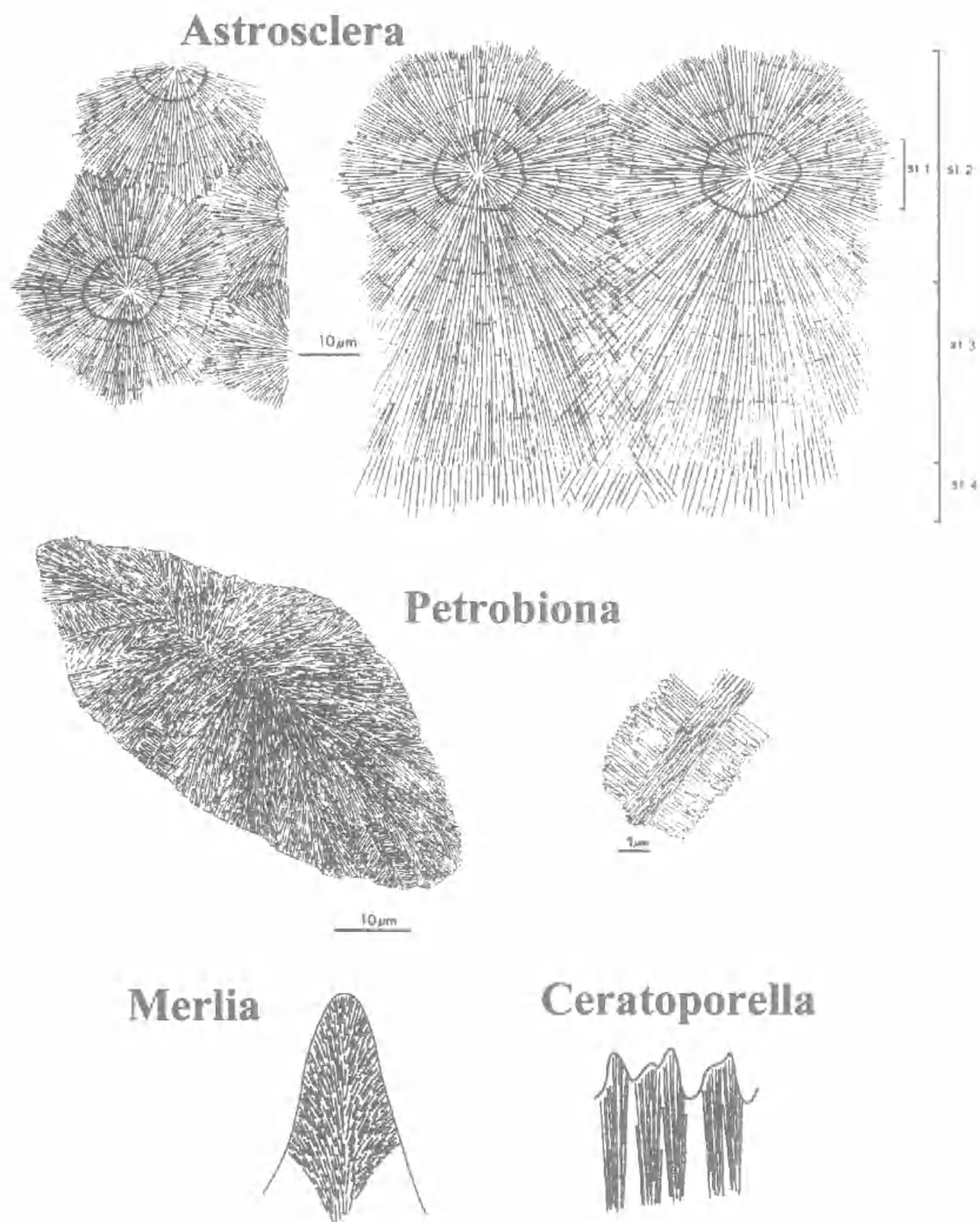


FIG. 4. Microstructural features of fibrous tissues in the skeleton of sponges of different systematic position. 'Spherulitic' microstructural type: *Astrosclera* (real spherulitic) and *Petrobiona* (fibro-radial microstructure) after P. Gautret, 1986; 'clinogonal': *Merlia*, (water-jet longitudinal arrangement of the fibers) and *Ceratoporella* (penicillate arrangement of the fibers) after J.P. Cuif & P. Gautret, 1993.

Thus, it is now possible to answer Cuif's first question positively. As for the second question, it appears that the specificity of intraskeletal structures confirms the phylogenetic value of the biomineralisation processes. Using these methods Cuif's group was able to provide precise definitions of microstructural elements for unresolved cases: 1) *Astrosclera* and the Triassic fossils *Follicatea*, developing from an unique center of mineralisation, with periodic growth by addition of prismatic units in the prolongation of similar units produced during the anterior growth stages, have typical spherulitic microstructure; 2) the *Calcarea Petrobia* and *Murrayonia* are characterised by composite microstructural elements with a continuous growth pattern of parallel fibril-like particles. No fossil forms are known at the moment with this type of microstructure.

For a long time the term 'clinogonal' has included the concepts of 'trabecular', 'water-jet' and 'penicillate' microstructures. Through accurate microstructural analysis Cuif & Gautret (1993) were able to show that these three types are distinct, and that the term 'clinogonal' is misleading and redundant. A 'water-jet structure' can be seen in *Merlia*, *Blastochaetetes* s. str. and *Chaetetes*; a 'penicillate' structure is seen in the Ceratoporellids (both Recent and fossil taxa); whereas true 'simple trabecular' microstructure has never been discovered in hypercalcified sponges (Fig. 3). Furthermore, chronologically there appears to be a synchronic alternating occurrence of microstructural types (spherulitic-astrosclerid-like; water-jet merliid-like; penicillate ceratoporellid-like), correlated with the alternation in skeletal aragonitic-calcitic mineralogy. These biological alternations correspond to the Sandberg thresholds (i.e. the repartition of the mineralogy of carbonate cements during the same geological time) (Fig. 4). The external constraints of oceanic parameters can influence the reactions by which calcium carbonate crystals are formed, although

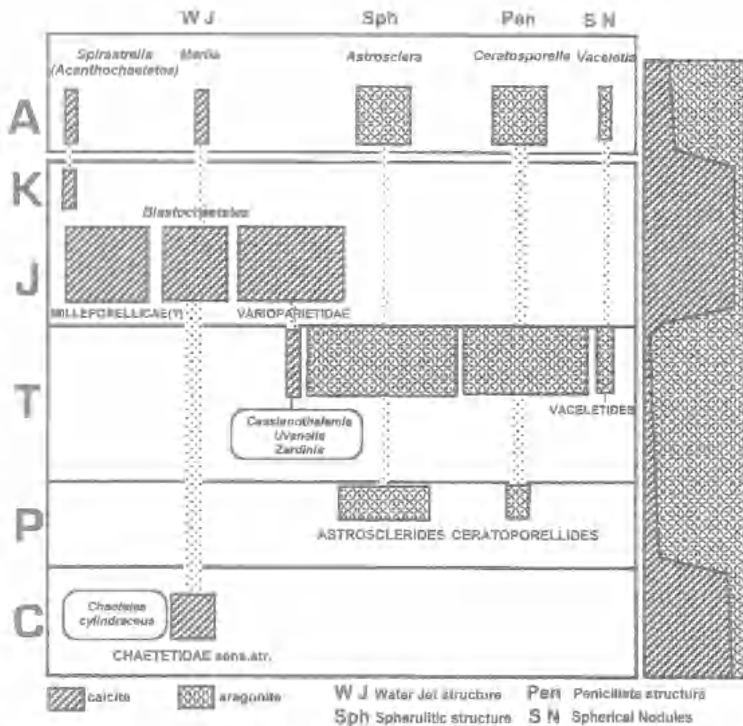


FIG. 5. Correspondence between skeletal mineralogy of sponges and deposits of carbonate sediments, after J.P. Cuif & P. Gautret, 1991, modified.

not the whole biological sequence of skeletal construction. During times when the water chemistry was unfavourable for mineral precipitation, sponges may have had only an entirely organic skeleton.

Diagenetic alterations affect mineral composition and microstructures, and this was one of the arguments previously used to dismiss the value of microstructural features for sponge systematics. This problem was carefully considered by the Orsay team (Marin & Gautret, 1994). The diagenesis of biogenic carbonates could not be solely estimated based on changes to the mineral phase. The amino acid content of the soluble organic matrices of different groups of sponges and other groups of fossils with hypercalcified skeletons, now required investigated.

Thus, the answers to Jean Vacelet's (1985) challenge could be obtained by palaeontologists, studying first the corresponding structures of living sponges, then applying these results to fossil sponges using the same methods, but applying necessary adjustments to compensate for diagenetic processes. Progress in these methods have been of mutual benefit to both palaeontologists and neontologists.



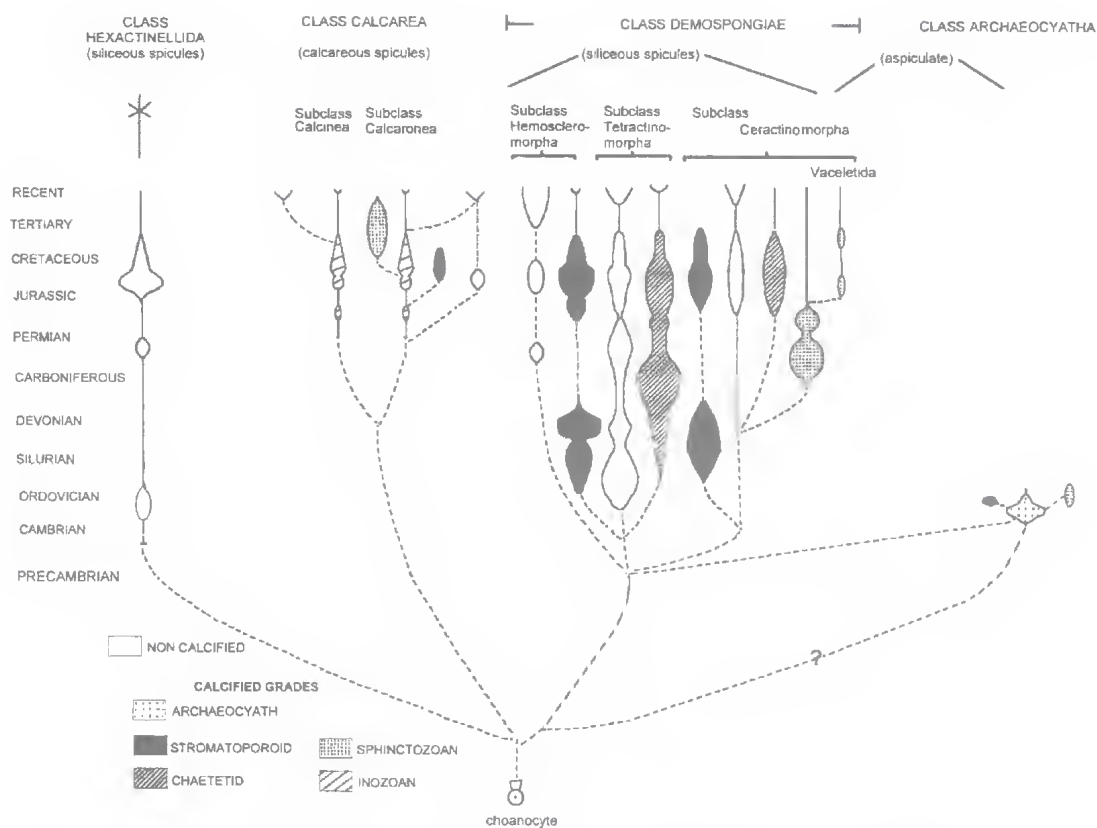


FIG. 6. Possible relationships of fossils and Recent sponges, after R.A. Wood, 1989, modified.

'THE PAST'. Fossil sponges might contribute to a better understanding of the history of the phylum, using palaeontological data to trace Recent families far back in time (Fig. 5). With the progress made in investigations into the terminal Precambrian and Lower Cambrian rocks (thanks to the successive international programs of IUGS since 1972), we can now trace the oldest preserved fossils (Fig. 6).

Only rare occurrences of hexactins have been found in pre-trilobitic sequences, in the Tommotian of Siberia and Meishucunian of South China. Genuine demosponge spicules are present in the upper Atdabanian as tetractines, with various additional elements in a much higher diversity than previously recognised, and some calcareous spicules are known from Australia (Bengtson et al., 1990). Calcified skeletons of archaeocyaths are present since the Tommotian. A cryptic pharetronid, *Gravestockia pharetronensis* Reitner, 1992, anchored on the inner wall of an archaeocyath cup and partially overgrown by its secondary skeleton, occurs in Atdabanian of Australia.

The discovery of Lower Cambrian soft fauna at Chengjian in Yunnan (Zhang & Hou, 1985) and at Shansha in Hunan (Steiner et al., 1993), containing completely preserved sponges, provide important indications on the origin and ecology of the first sponges. After arthropods, sponges represent the most diverse metazoan group in the Chengjiang fauna, with at least 11 genera and 20 species of hexactinellids (Chen & Erdtmann, 1991; Rigby & Hou, 1995). Those described previously as demosponges are also now considered to be hexactinellids (Reitner & Mehl, 1995). The soft bodied Chengjiang sponges, embedded in mudstone layers of a low-energy environment, displayed different architectures and they represent a sessile, suspension-feeding epifauna.

Precambrian remains were under discussion for a long time. Of the many reported spicules from proterozoic sediments most have proven to be volcanic shards, or other inorganic crystals, apart from some indubitable spicules from the Upper Precambrian of China. Until recently the oldest sponges known were late Ediacarian

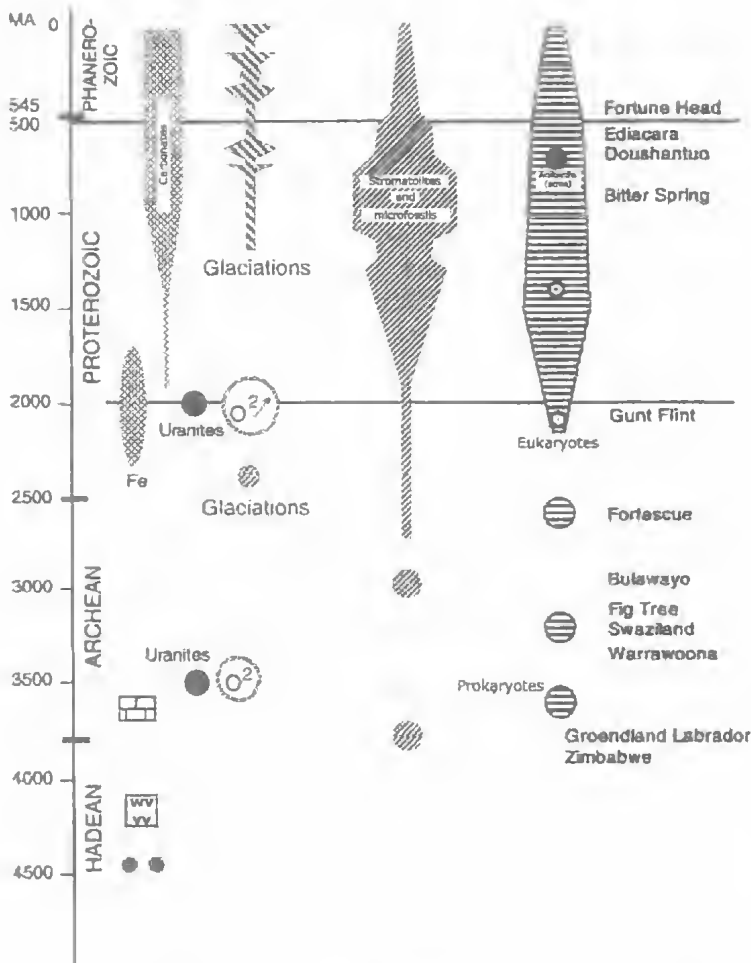


FIG. 7. Biotic and abiotic events since the Earth formation; position of the first fossil assemblages (Doushantuo & Ediacara) containing sponge remains.

hexactinellids, *Paleophragmodictya* (Gehling & Rigby, 1996), characterised by disc shape impressions preserving characteristic spicular network. This sponge is slightly older (565my) than the 'Cambrian explosion' (545my), when practically all the principal animal phyla appeared over a period of a few tens of million of years in the form of skeletised bodies. More recent discoveries in Weng'an, China, of spectacularly preserved embryos and tissues in rocks that are about 570my old, provide new data for the early animal evolution and particularly for sponges.

Since Haeckel (1877) it was thought that sponge ancestors might have been microscopic, soft bodied, and therefore not preserved in the

fossil record. Now such fossils have been found in Doushantuo phosphorites (Xiao et al., 1998): the constant size of fossils, irrespective the number of compartments they have (two-cell stage; four-cell stage; polyhedral blastomeres) fits a pattern of developing early embryos with a constant cytoplasmic volume. Li, Chen & Hua (1998) figured and described a tubular and globular phosphatised sponge, some plasmolised epidermal cells, a young morula with spherical blastomeres, some embryos at the blastula stage, a parenchymella larva with peripheral flagella, a less convincing fragment of an amphiblastula larva, and a bud connected to its parent. They interpreted these as sponges: the needle shaped spicules in Doushantuo sediments are regularly arranged in distinct bodies built up of cell-like objects, some of which adhere to the spicule, much the same way as sclerocytes do in living sponges. Preserved soft tissues found in the Doushantuo material include sclerocytes, porocytes, amoebocytes; the most abundant fossilised embryos were at the blastula

stage of development; three specimens were identified as parenchymella larvae with preserved flagella (demosponges); and the putative presence of one amphiblastula suggests that the calcareous sponges may extend into the Precambrian.

THE FUTURE OF THE PAST. This is a small precis of what can be said about fossil sponges, their connections to Recent ones, and of the interactions between the two domains. Other topics are now promising: the history of reef-building, the evolution of their communities, the influence of nutrients and predators (Wood, 1993; 1995), and the importance of the cryptos since the Cambrian (Wood & Zhuravlev, 1993).

Advances in molecular biology, sequencing and gene cloning applied to well-chosen Recent sponges is a promising new path for research. The ability to apply these techniques to some fossil material has already been demonstrated, although the highly degraded nature of 'fossil DNA' makes the choice of the material critical, and careful attention must be paid when interpreting group relationships. As in the past, in the future there is hope of discovering new and exciting fossil material. We are only at the beginning of investigations into the Precambrian phosphorites, in which were found the exceptional record of early multicellular life. Precambrian phosphorites containing soft cellular tissue and embryos preserved in calcium phosphate, equivalent of Doushantuo Formation, are known throughout the world. It is hoped that their continued investigation will offer endless resources for a new comprehension of primitive evolution of animal life. Are palaeoembryology and palaeohistology the future of Palaeontology?

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